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Enemy Behind the Gates? Predicted Climate Change and Land-Use Intensification Likely Speed Up C4 Grass Invasions in Europe

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ABSTRACT

Aims: Climate change is expected to bolster opportunities for alien species' establishment and spread. In Europe, alien C4 grass species have the potential to benefit from a changing climate, being better adapted to higher temperatures and heat stress. Our aim was to compile an up-to-date inventory of alien C4 grass species in Europe, to find information about their distribution and country- and region-wise statuses, to identify the most widespread and high-risk species, and the most invaded habitat types, and to draw the temporal trends of their European establishment.

Location: Europe.

Methods: We used the standard systematic literature review methodology to identify relevant publications and online plant distribution databases to get an up-to-date list of alien C4 grass species in Europe. We aimed also to gather information on (1) their current country- and region-wise distribution; (2) alien status in each country (casual, naturalised, invasive); (3) the most widespread and high-risk species; (4) native climatic zones and habitat preferences of each species in European countries; and (5) temporal distribution patterns of the identified species.

Results: We detected 133 alien C4 grass species across Europe, with the highest number of species in western European countries (103 species) and the lowest in northern Europe (69 species), with considerable overlap amongst regions. Southern Europe stands out with the highest number of naturalised (55) and invasive (21) species compared to other regions, while northern Europe has the highest number of casual species (53). We identified the most widespread and high-risk species, including those from tropical and subtropical climatic zones, which pose the highest invasion risks. These species pre-dominantly occur in ruderal and anthropogenic habitat types, but also in natural habitat types, especially in grasslands.

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Regarding temporal trends, we detected an alarming increase in the establishment of tropical C4 grasses in Europe in recent decades.

Conclusions: Many European countries already harbour a high number of C4 grass species, but with different alien statuses. Besides climate and invasion potential, human activities are also important factors in the ongoing invasion process of alien C4 grass species. Collective actions are required to halt this alarming biodiversity problem.

1 | Introduction

The spread of invasive plant species and climate change are interconnected threats to the biodiversity of natural ecosystems, affecting also societal structures and global governance practices, and the magnitude of their long-run effect extends far beyond their current level (Bradley et al. 2010; Burgiel and Muir 2010; Singh et al. 2023). Invasive plant species pose a significant threat as they can outcompete native flora, disrupt habitat structure and interfere with biological processes (Castro-Díez et al. 2016). Climate change exacerbates this problem by creating new environmental conditions that may favour the spread and establishment of these invasive plant species (Bradley et al. 2010). Warmer temperatures, altered precipitation patterns and increased frequency of extreme weather events can facilitate the invasion of alien plants into new regions (Vilà et al. 2007; Thuiller et al. 2008; Finch et al. 2021). This dual threat introduces new dynamics, precipitating a sudden and irreversible transformation of interactions amongst native and invasive plant species (Richardson et al. 2000). Therefore, to fully grasp the implications of climate change on invasive plant species, it is crucial to consider how a changing climate influences the movement of plant species across barriers and through different stages of invasion (Catford et al. 2012, 2019; Catford and Jones 2019; Gioria et al. 2023). Understanding the specific implications of climate change for each stage of invasion is essential for supporting management actions aimed at minimising introductions and mitigating the negative impacts of establishing alien plant species in time (Blackburn et al. 2011).

Climate change has both direct and indirect effects on the dispersal and establishment of invasive plant species (Vilà et al. 2007; Thuiller et al. 2008; Bradley et al. 2010; European Environment 2017). The changes in the abiotic (e.g., temperature, precipitation) and the biotic environment (e.g., distribution range shifts or altered phenological patterns of native species) related to climate change may confer direct benefits to invasive plant species compared to resident native ones (Capdevila-Argüelles and Zilletti 2008; Finch et al. 2021; Lopes et al. 2023). At the same time, climate change indirectly disrupts processes, imposes stress on native species, alters the frequency and nature of disturbances and reshapes species interactions, all of which collectively furnish openings for the proliferation of invasive species (Finch et al. 2021; Lopes et al. 2023). Besides, facing climate change, invasive plant species tend to increase their growth and productivity (Robinson et al. 2020) and exhibit greater plasticity compared to their native counterparts (Gentili et al. 2021). Their spread is likely facilitated by disturbances, such as those arising from land use alterations, which provide them opportunities at the expense of native species, which may be less preadapted to changes in their environment (Pyankov et al. 2010; Chuine et al. 2012). Therefore, the anticipated effects of climate change, including rising temperatures and CO_2 levels (Amare 2016), are projected to bolster opportunities for invasive plant species. However, experimental studies showed that invasive plant species may respond unpredictably in the face of different components of climate change acting simultaneously, which adds uncertainty to predicting the path of invasive species (Robinson et al. 2020).

In Europe, the IPCC Sixth Assessment Report (2023) projected a significant warming across the continent, with high variations in its impact by regions. Southern Europe is projected to experience strong summer warming, while northern Europe will be subjected to the highest winter temperature increase. These projections are expected to become more noticeable by mid-century, with further intensification by the end of the century. The specific periods when these changes will become most apparent are typically the mid-term (2041–2060) and long-term (2081–2010) horizons (Lee et al. 2023). An increasing amount of precipitation is expected in northern Europe, and a decrease in certain areas of southern Europe throughout all seasons (European Environment Agency 2021), with a very likely precipitation decrease in the summer months in the Mediterranean region (Coppola et al. 2021). Western and eastern Europe are expected to experience extreme precipitation changes in autumn, winter and spring, while facing reduced rainfall during the summer (European Environment Agency 2021). As a result of this, the risk of summer droughts is likely to increase in most European regions with temperate climates, but this trend would be even more marked in the Mediterranean areas also due to warmer summer temperatures. Indeed, the Mediterranean region of southern Europe stands as a focal point of climate variability compared to eastern, western and northern European countries (Walther et al. 2009; Brunel et al. 2010; Navarra and Tubiana 2013; Kovats et al. 2014; Drobinski et al. 2020). In the Mediterranean, biological invasions are rising fast (Celesti-Grapow and Ricotta 2021), mainly by plant species originating from regions with similar climates (Cao Pinna et al. 2021, Cao Pinna et al. 2024), which allows them to establish more easily than plant species from dissimilar climates.

The climate change patterns of Europe have the potential to foster the invasion of one particular group of species, namely the alien C4 grass species, because they have often been cited as beneficiaries of actual environmental changes (Chuine et al. 2012; Kumar et al. 2017; Boretti and Florentine 2019). Plant species with the C4 photosynthetic pathway make up only a tiny part of the native vascular flora of Europe (up to 0%–2%, Collins and Jones 1986). However, their number is increasing due to the establishment of alien C4 species mostly with tropical and subtropical origins (Pyankov et al. 2010). Notably, nearly 1.5% of the total alien vascular flora of Europe are C4 grass species, as identified by Kalusová et al. (2024), who documented 7335 alien vascular species in the region. The response of C4 species to elevating CO_2 levels and climatic

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conditions can greatly vary compared to the C3 photosynthetic pathways based on their inherent physiological characteristics and the specific environmental context (Bernacki 2012; Wang et al. 2020). The C3 grasses, such as *Triticum aestivum* (wheat) (Law and Crafts-Brandner 2001) and *Oryza sativa* (rice) (Uprety et al. 2002), initially benefit from elevated atmospheric CO_2 as it enhances the effectiveness of their photosynthesis (Wang et al. 2020); however, prolonged exposure may lead to reduced nitrogen-use efficiency and offset these gains. Conversely, C4 species, exemplified by *Zea mays* (corn) and *Saccharum officinarum* (sugarcane), exhibit a more efficient carbon fixation mechanism, making them comparatively resilient in arid and high-temperature environments, although with diminishing advantages as CO_2 concentrations rise (Sage and Kubien 2003; Kumar et al. 2017; Boretti and Florentine 2019; Salesse-Smith et al. 2025). This is because C4 plants already concentrate CO_2 in specialised cells, known as bundle sheath cells, which reduces their reliance on ambient CO_2 (Sage and Kubien 2003; Bouchenak-Khelladi et al. 2009; Edwards and Voznesenskaya 2011; Kumar et al. 2017; Havrilla et al. 2023). To understand how various plant types will respond in a changing climate, it is crucial to consider multiple factors, such as temperature, water availability and nutrient status (Gritti et al. 2006; Bernacki 2012; Sales et al. 2021).

The spread of C4 invasive species, including several grasses, has already been highlighted in Europe (Collins and Jones 1986; Mateu 1992; Pyankov et al. 2010; Appendix S1), and their increasing number is supposedly linked with the climate-driven introduction and spread of C4 alien species (Pyankov et al. 2010; Chuine et al. 2012). Thriving mainly in croplands and plantations, alien C4 grass species such as *Sorghum halepense* (Follak and Essl 2013) and *Paspalum distichum* or *Eleusine indica* (Alcantara et al. 2016) may seriously impact agriculture. Other alien C4 grasses gradually infiltrate degraded and semi-natural habitats. In Hungary, for instance, sand grasslands were invaded by *Sporobolus cryptandrus* (Török and Aradi 2017; Török et al. 2021) and *Sporobolus indicus* (Bauer and Verloove 2023). These examples of expansions of invasive grass species not only present challenges to local ecosystems and agriculture, but their ability to evolve herbicide resistance makes them more resilient and difficult to control, posing on-going challenges for conservation efforts and agricultural practices (Fernando et al. 2016).

This study aims to explore the current distribution patterns of alien C4 grass species across European regions and countries, reviewing published literature and online available databases. In particular, we aimed to (1) gather information on the current European distribution, number of species and country-wise densities of detected alien C4 grass species; (2) compare European regions and countries regarding the alien statuses of C4 grass species (casual, naturalised, invasive); (3) identify the most widespread and high-risk alien C4 grass species; (4) identify the native climatic zones and the habitat preferences of each species in European countries and (5) assess the temporal distribution patterns of the identified species. Through these efforts, our ultimate goal was to offer valuable insights for the understanding of current invasion patterns of alien C4 grasses in Europe, which might serve as a basis for predicting future trends. This research forms a necessary starting point for subsequent studies aimed at comprehensively addressing and managing the impact of C4 grass invasions in Europe.

2 | Materials and Methods

2.1 | Compilation of the List of Alien C4 Grass Species for Europe

During the identification of relevant studies and publications on alien C4 grass species in Europe, our search encompassed research articles, reports and documents published in peer-reviewed journals in English and authoritative online databases. Google Scholar and ISI Web of Science were used as primary sources for the literature search, while we used further databases to extract information about the identified alien C4 grass species: EURO+MED PlantBase, the European Distributed Institute of Taxonomy (Euro+Med 2023); Royal Botanical Garden Kew's Plants of the World Online (POWO 2023); CABI Compendium Invasive Species (CABI 2023), GloNAF—Global Naturalised Alien Flora (GloNAF 2023); (PADAPT) Pannonian Database of Plant Traits (Sonkoly et al. 2023); and GBIF—Global Biodiversity Information Facility (GBIF 2023). The last database was used to verify scientific names and unify synonyms.

To refine our search and identify the most pertinent studies and sources, we used all the possible combinations of the following three keyword groups: (1) alien status (alien, non-native, introduced, neophyte, casual, naturalised, potentially invasive and invasive), (2) C4 grass species (C4 grass, Poaceae or grass) and (3) the names of the 39 European countries and two islands treated separately (see below). Boolean operators (AND, OR) were used to refine search results. The resulting search terms looked like: 'alien' OR 'introduced' OR 'neophyte' OR 'casual' OR 'naturalised' OR 'potentially invasive' OR 'invasive' AND 'C4 grass' OR 'Poaceae' OR 'grass' AND 'COUNTRY NAME'.

The identified alien C4 grass species were classified into three categories using the definitions of Richardson et al. (2000): casual (introduced alien species without self-sustaining populations), naturalised (alien species with self-sustaining populations), or invasive (naturalised species that have the potential to spread over a considerable area). For the assessment of these statuses for each species, multiple databases (all platforms mentioned formerly), along with relevant scholarly papers, were reviewed carefully, considering the characteristics and behaviours of each species as described in the literature. In cases where the literature did not explicitly define the category, we evaluated the species based on its rapid growth, establishment, spread patterns and its degree of presence in the new area. To streamline the process, the most severe alien status for each species was selected within countries and European regions, ensuring consistency with the definitions provided by Richardson et al. (2000).

Furthermore, we collected information about the current European distribution of the identified alien C4 grass species in all 39 European countries. In addition, we considered the Canary Islands and Corsica independently, despite being

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politically affiliated with Spain and France, respectively, because of their markedly different geographical locations and climates compared to the mainland territories to which they are politically connected. Then, countries were grouped into distinct regions within Europe: northern Europe, western Europe, southern Europe, or eastern Europe based on the United Nations (UN) geoscheme created by the UN Statistics Division (United Nations Geoscheme 2024).

The native distribution range of the species was extracted from the Plants of the World Online database (POWO 2023), based on which we categorised the species into temperate, subtropical or tropical climatic origins.

To identify the most vulnerable European habitat types subjected to the spread of alien C4 grass species, we conducted a keyword-based literature search for each identified species in all European countries where the species occurred. As the quality of habitat information found for these species was highly versatile, we used the EUNIS (European Nature Information System) Habitat Classification, a widely used hierarchical classification of European habitats. We referred only to inland and terrestrial habitats; therefore, marine and inland surface water habitats were excluded. We defined our categories based on EUNIS Level 1, i.e., the highest level of the classification hierarchy, but we considered the sublevels of these categories as proposed by Chytrý et al. (2020). However, as an exception, we split one Level 1 category into two categories (Regularly or recently cultivated agricultural, horticultural and domestic habitats) to accurately characterise the habitat preference of the ruderal C4 grass species. Our categorisation included the following main habitat groups: (1) Coastal habitats (dunes, shingle, rock/cliffs); (2) Wetlands (mires, bogs and fens); (3) Grasslands and lands dominated by forbs, mosses or lichens (dry, mesic and wet grasslands; alpine and subalpine grasslands, woodland fringes and clearings and tall forb stands, inland salt steppes, sparsely wooded grasslands); (4) Heathland, scrub and tundra (arctic, alpine and subalpine scrubs, temperate and Mediterranean scrubs, temperate heathland); (5) Forests and other wooded land (broad-leaved and conifer woodland and plantations; lines of trees, small anthropogenic forests, recently felled forest, early-stage forest and coppice); (6) Inland un-vegetated or sparsely vegetated habitats (rock/cliffs, scree, caves); (7a) Regularly or recently cultivated agricultural, horticultural and domestic habitats (including arable land and market gardens, fallows and recently abandoned arable lands); (7b) Artificial grasslands and herb-dominated habitats (including agriculturally improved, re-seeded and heavily fertilised grassland, including sports fields and grass lawns, trampled grasslands with annuals, annual anthropogenic herbaceous vegetation); (8) Constructed, industrial and other artificial habitats (buildings of settlements, transport networks, industrial sites, waste deposits). Note that the quality of habitat information found for the species was highly versatile, and we found no habitat information for many newly established species.

Nomenclature challenges posed significant difficulties in harmonising our species list with the previous ones, due to the species having different names in the past and numerous synonyms. To solve this, we verified the scientific names with careful attention to unifying the synonyms across many databases. Our species list follows the nomenclature of the Global Biodiversity Information Facility (GBIF 2023).

2.2 | Data Synthesis and Analysis

The total number of alien species and their alien statuses (casual, naturalised, invasive) were calculated for each European country separately, and also for the European regions by summing up the 'worst' status of each species. Subsequently, the species density of alien C4 grasses in each country was calculated by dividing the total number of alien C4 grass species occurring in the country by the land area of the given country in km^2. The number of alien species originating from different native climatic zones (temperate, subtropical, tropical) was also calculated for each country. We applied chi-squared tests of independence to determine whether the distribution of species with different invasion statuses (casual, naturalised, invasive) differed across regions of Europe and also to determine whether the distribution of species with different climatic origins (temperate, subtropical, tropical) differed across these regions. As a post hoc test, we performed pairwise binomial tests within each region with Bonferroni corrections.

To identify potential drivers of invasion and the relationship between the number of species with different statuses (casual, naturalised and invasive), linear regression models were used. We assessed whether the number of casual species is related to the number of invasive species and whether the number of naturalised species is related to the number of invasive species in each European region. These relationships may explain the dynamics of alien species establishment and their transition to invasive status, which are important factors for understanding regional trends. The analyses were done in R version 4.3.2 (R Core Team 2023), with data manipulation handled through the 'dplyr' package and visualisations generated using 'ggplot2' package.

To identify the most widely distributed alien C4 grass species in Europe, we counted the number of countries where each species was found. We call this measure "European distribution". Besides, we also ranked the species based on their invasion risk based on their current distribution range and alien status across European countries. First, we assigned ranks to each species in all countries they were introduced to, based on their current alien status: casual = 1, naturalised = 2, invasive = 3. Second, we calculated the rank sum for each species: we summed up the ranks assigned to each species in the four European regions separately. High rank sums indicate that a species is not just widely distributed but also has invasive status in many countries. We identified the most widely distributed species and the high-risk species both at a continental scale and in the four European regions separately.

To compare the species-pool similarity/dissimilarity of the four European regions regarding the presence of widespread alien C4 grass species, a Detrended Correspondence Analysis (DCA) was performed on 39 countries (excluding Corsica and the Canary Islands represented with very few species). DCA was calculated on ordinal datasets of species (each species was included using

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the 'worst' alien status in the respective country—i.e., 1 = casual, 2 = naturalised and 3 = invasive) to visualise the variation in species data. DCA was calculated using Canoco 5 (Šmilauer and Lepš 2014).

We also compared three published lists of species (Collins and Jones 1986; Mateu 1992; Pyankov et al. 2010) with the current species list to analyse trends over time to see if the number or status of alien C4 grass species is increasing, decreasing, or remaining stable in Europe. Because of the nature of the data and the small sample size, which did not make statistical analysis possible, we could only visualise the trends.

3 | Results

3.1 | Distribution of C4 Grass Species Across European Regions and Countries

Our database of alien C4 grasses contained 133 species in 39 European countries and two independently treated islands (Corsica and the Canary Islands). The species had highly varying invasive statuses across different countries and regions. For further details, check Appendices S4 and S5. We found the highest number of alien C4 grass species in western Europe (103 species), followed by southern (96 species) and eastern Europe (81 species), while the lowest number of species was detected in northern Europe (69 species) (Figure 1, Appendix S5). When considering the number of alien C4 grass species at the country level, we found the highest number of species in the southwestern part of the continent: Spain (69 species), Italy (65), Belgium (65), France (64) and the United Kingdom (60). The countries of the Balkan Peninsula and of the northern and northeastern parts of the continent hosted comparatively low numbers of species. Iceland hosted only one alien C4 grass species: *Digitaria ischaemum* (Figure 1, Appendix S4).

Regarding the C4 alien grass species density per 1000 km^2, we observed some regional patterns, with higher densities in southern and western Europe (Figure 2). Liechtenstein had the highest recorded density of alien C4 grass species, due to its highly limited size (8 species in just 160 km^2). Amongst the western European countries, Belgium, Luxembourg and Switzerland also showed high densities of C4 grass species. Kosovo hosted the highest C4 grass density in southern Europe, followed closely by Montenegro and Slovenia. However, we found southern countries with low densities as well, such as Spain or Portugal. Conversely, northern and eastern Europe tended to have lower species density, with Iceland and Ukraine having the lowest C4 alien grass species densities in these regions. Sweden and Finland also presented very low densities of alien C4 grass species, reflecting the broader trend of reduced species density in northern Europe (Figure 2).

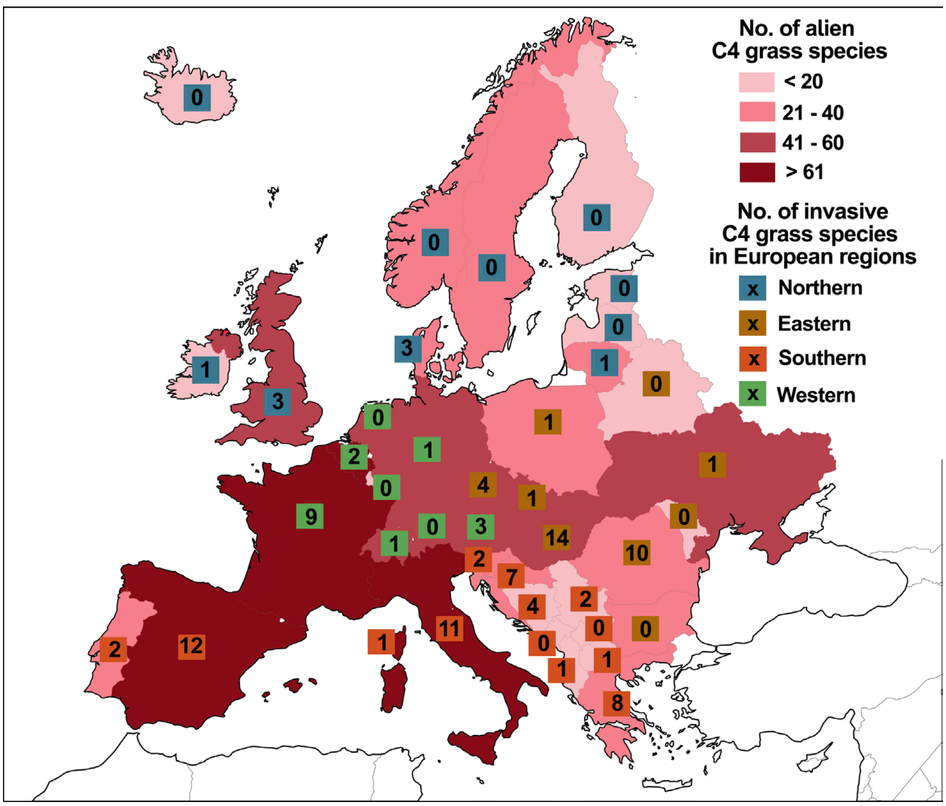

FIGURE 1 | Number of all alien and invasive C4 grass species in European countries and regions. The number of alien species is indicated by the colouring of a country in a shade of red, while the number of invasive alien species per country is indicated in a coloured square. The colour of squares indicates the region the countries belong to: northern (blue), eastern (brown), southern (orange) or western Europe (green). The Canary Islands with one invasive species out of three alien species are not shown in the map.

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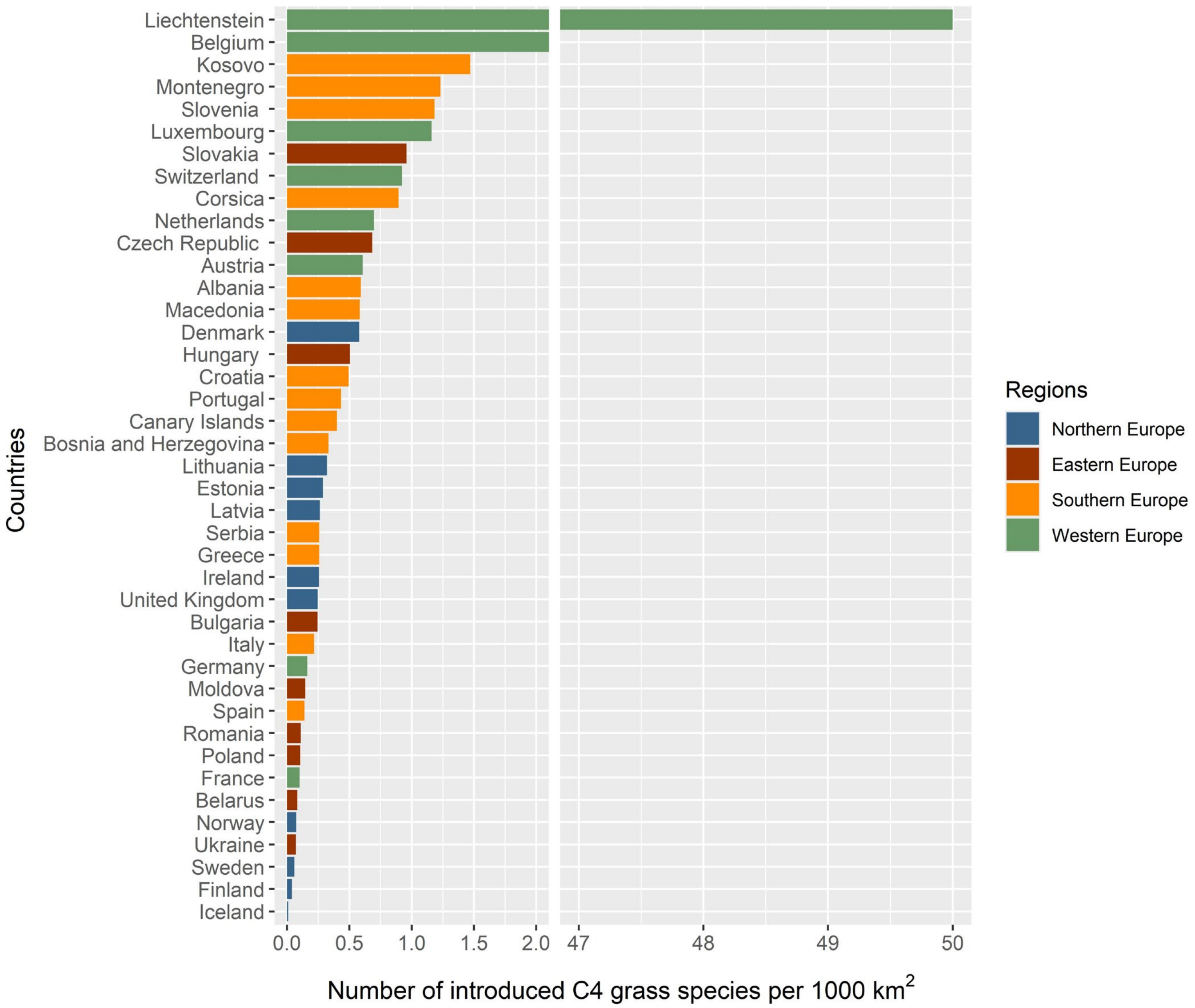

FIGURE 2 | Species density of C4 alien grass species across European countries and regions (number of species per 1000 km^2).

3.2 | Alien Statuses per Region and Country

We found regional variations in the prevalence of casual, naturalised and invasive C4 grass species. The chi-square test ($\chi^2 = 46.7$, $p < 0.001$) indicated that the distribution of species with different invasion statuses differs significantly amongst regions (Figure 3a). Southern Europe stands out with the highest number of naturalised species compared to other regions, while northern Europe had the highest number of casual species and a very low number of invasive species. Western Europe also had a high number of casual and naturalised species but a significantly lower number of invasive species. The numbers of species with different statuses in eastern Europe were not significantly different (Figure 3a).

When analysing the alien C4 grass species' invasive statuses per country, we found high variations within regions. Hungary had the highest number of invasive species, followed by Spain and Italy (Figure 1). Naturalised species were especially abundant in western and southern Europe. Casual species had notable counts in Belgium, the United Kingdom and the Czech Republic. Some countries with a low number of alien C4 grass species, like Moldova, Iceland and Luxembourg, do not have reported invasive C4 grass species at all (Figure 1). For more details, check Appendix S4. Interestingly, 39 C4 grass species had varying statuses across different regions or even within the same region.

The current number of casual C4 grass species was not significantly related to the number of invasive C4 grass species in either of the four regions of Europe. The number of invasive species was more strongly related to the number of naturalised species, and this relationship was positive and significant in most regions. Detailed results are available in Appendix S2.

3.3 | The Most Widely Distributed and High-Risk Species of Europe

We identified the most widely distributed and high-risk species in Europe based on their current distribution and alien statuses in European regions and countries. Amongst the 133 species listed in our database, 40 species (nearly 30%) were present in all four regions of Europe. We identified 14 species

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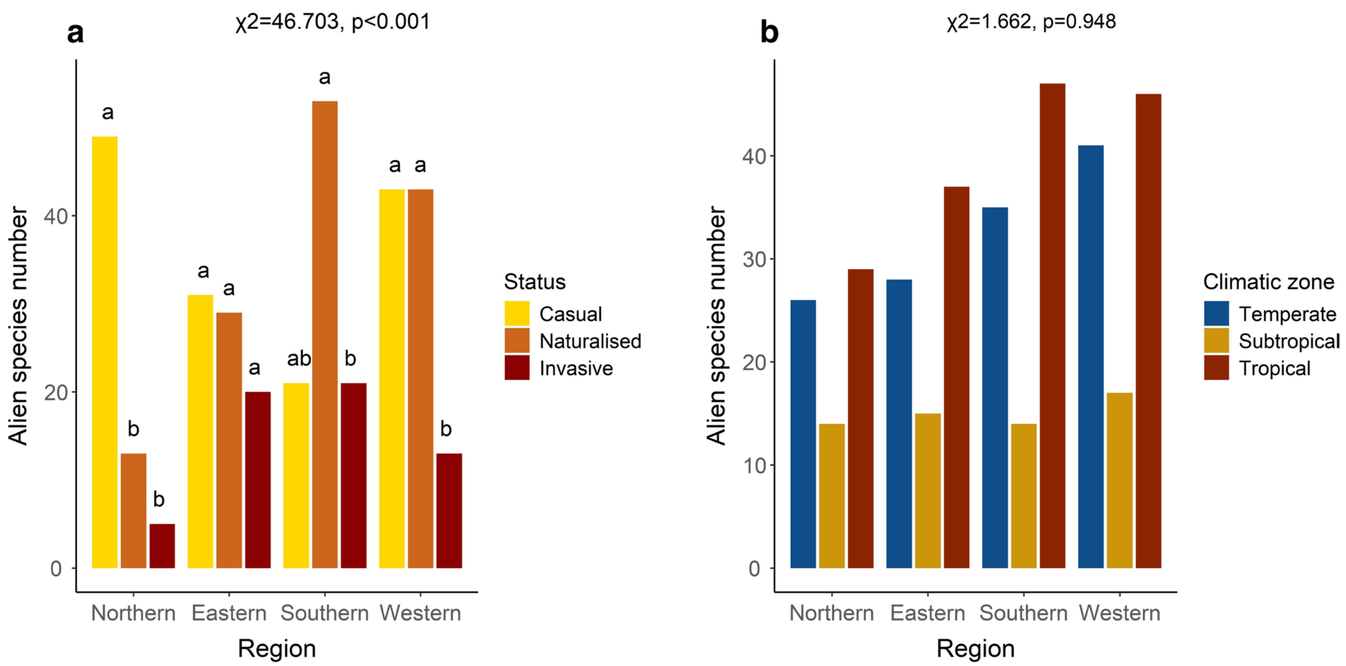

FIGURE 3 | The number of C4 alien grass species categorised by (a) their alien status (casual, naturalised, invasive) and (b) their climatic origin (tropical, subtropical, temperate) across four different European regions (northern, eastern, southern, western). Chi-squared tests were used to test if there are significant differences in the regional distribution of the species with varying statuses and climatic origins. Significant differences within regions according to post hoc pairwise binomial tests are indicated by different superscript letters.

within this subset with the highest total rank sum (≥ 35), considering them as species with the highest risk due to their wide distribution and frequent invasive statuses in European countries. The identified species in the order of total rank sums are as follows: *Eleusine indica, Panicum capillare, Sorghum halepense, Panicum miliaceum, Panicum dichotomiflorum, Setaria italica, Cynodon dactylon, Setaria faberi, Setaria verticillata, Zea mays, Paspalum distichum, Digitaria ciliaris, Echinochloa crus-galli* and *Sorghum bicolor*. For more details, check Appendix S6.

Species frequently ranked as 'invasive' but with limited distribution, should also be highlighted, as they can be expected to become invasive in other countries in the future. For example, *Andropogon virginicus* was found only in France, where it is considered invasive, while *Sporobolus pyramidalis* is present only in Slovakia and is also considered invasive there. This trend is further explored in Appendix S6. The southern European region is the most unique regarding the alien C4 grass species composition compared to the other regions. Southern Europe has several invasive species that are widespread in the countries of this region but are not present or are only casual or naturalised in other regions, such as *Paspalum distichum*, *Paspalum dilatatum*, *Cenchrus longisetus* and *Sporobolus elongatus*. Please refer to Appendix S3 for a detailed description of the species pool analysis.

3.4 | Origin and Habitat Preferences of Alien C4 Grass Species

The number of C4 alien grass species with different origins (tropical, subtropical, temperate) was not significantly different in the four regions of Europe ($\chi^2 = 1.7$, $p = 0.948$). In all regions, similar numbers of species originated from tropical and temperate zones, and considerably fewer species from subtropical zones (Figure 3b).

Our extensive data search provided some insights into the European habitat preferences of 95 out of the 133 alien C4 grass species. For most species with available habitat preference data, one (24%), two (30%) or three (27%) habitat types were listed. Only 19% of the species were present in more than three habitat categories, with *Ehrharta erecta* having the most versatile habitat preference, being present in seven habitat categories. Most C4 grass species occurred in various ruderal and anthropogenic habitats, particularly in artificial grasslands and herb-dominated areas. These included trampled grasslands, ruderal roadside vegetation and lawns (51 out of 95 species), as well as constructed, industrial and other artificial habitats (48 out of 95 species). A high number of species were also found as weeds in cultivated or agricultural areas (Figure 4). Amongst species of natural or semi-natural habitats, most colonised grasslands (39 species), while fewer were found in forests (16 species) or wetlands (18 species) (Figure 4). For further information, check Appendix S7.

3.5 | Temporal Changes in the C4 Grass Species List in Europe

We compared the compiled list with three comprehensive lists of European C4 species published in 1986, 1992 and 2010, and we found a considerable increase in the number of alien C4 grass species in the last decade (Figure 5). According to these lists, there are four distinct groups of alien C4 grass species: (1) old introductions:

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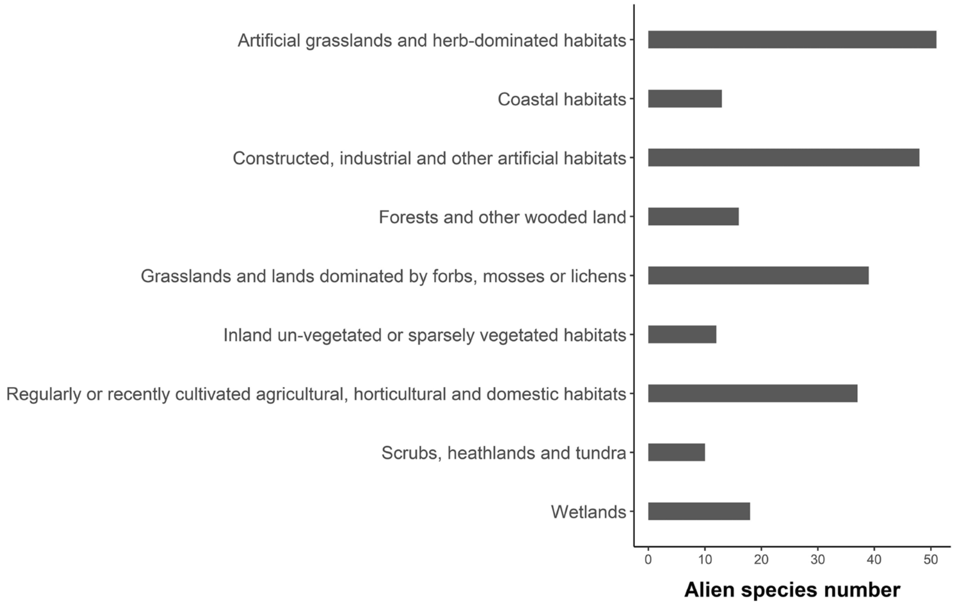

FIGURE 4 | The number of C4 alien grass species in each of nine inland and terrestrial EUNIS habitat types in Europe. Most of the species occurred in more than one habitat type.

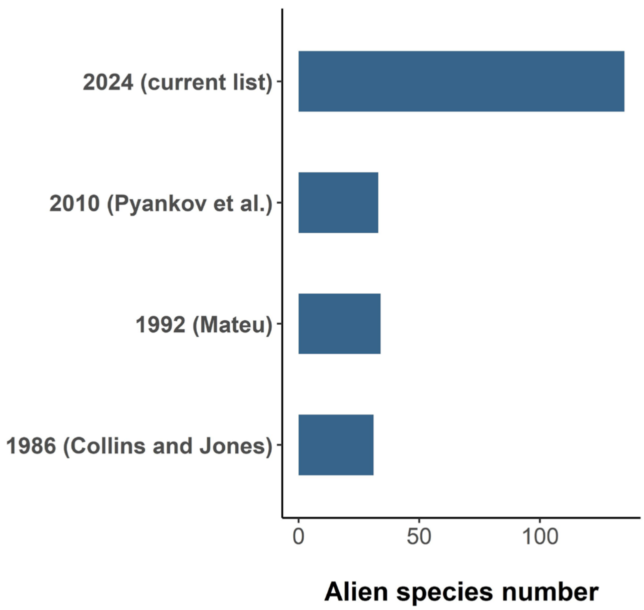

FIGURE 5 | Temporal changes in the number of C4 alien grass species in Europe according to three published lists and the current study.

alien species that have been reported from Europe before 1986. We found 30 such species, e.g. *Cenchrus ciliaris*, *Echinochloa crus-galli*, *Sporobolus indicus* and *Sorghum halepense*; (2) new introductions: species that were not mentioned by Collins and Jones (1986) but appeared in the later lists of Mateu (1992) and/or Pyankov et al. (2010), 10 species, e.g. *Cenchrus longispinus, Miscanthus sinensis* and *Paspalum urvillei*; (3) recent introductions: species that were not mentioned in former lists but appeared in our current list; 70 species, e.g., *Andropogon virginicus, Chloris barbata* and *Ehrharta calycina*; (4) range-expanding species: species that were listed as natives in Europe by these previously published lists, but they colonised new European countries where they are considered to be alien; 25 species, e.g. *Tragus racemosus, Eriochloa villosa* and *Sporobolus alterniflorus*. For further information, check Appendix S1.

4 | Discussion

The C4 photosynthetic pathway evolved in tropical climates and shows improved performance at high temperatures as supported by physiological measurements and their concentrated distribution in tropical areas (Griffith et al. 2015; Watcharamongkol et al. 2018). However, C4 grass species have no physiological barrier to expanding into temperate or cooler regions, but geographical barriers and lack of opportunities prevented their colonisation until recently (Watcharamongkol et al. 2018). Global climate warming and facilitated biotic exchange amongst regions due to global commerce opened the door for the homogenisation of C4 grass flora amongst different climatic regions (Olden et al. 2004; Jia et al. 2016). Therefore, it is not surprising that our findings suggest a rising trend and high variability in alien C4 grass invasions across Europe. Western Europe had the highest number of alien species (103), while southern Europe had the largest numbers of naturalised species (55) and invasive species (21) indicating high invasion pressure. On the contrary, northern Europe had low densities throughout invasion statuses with casual species dominance.

4.1 | Distribution of Alien C4 Grass Species in Europe

The current distribution of alien C4 grasses across European regions shows a clear species richness hotspot in the south-western part of the continent. This distribution is partly explained by climatic factors, but variations within the regions suggest that biogeographic, historical and socio-economic factors also influence the pattern (Pyšek et al. 2022a). The highest number of alien C4 grass species found in Spain, Italy, France

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and Belgium can be attributed to many different factors. (1) The Mediterranean and oceanic climate of these countries with mild, less frosty winters can support the establishment and performance of C4 grasses. (2) These countries have been centres of alien plant exchange and colonisation due to trade and migration for centuries (Celesti-Grapow et al. 2009). (3) Greater national wealth is also often linked to a high number of alien species (Pyšek et al. 2022a) because wealthy countries have historically served as gateways for their introduction. This is due to their strong overseas relationships, long history of horticulture and ornamental plant trade (Arianoutsou et al. 2021), and, in the case of C4 grass species, growing interest in their use as energy crops (Lewandowski et al. 2003). (4) The number of species documented in a country is presumably also influenced by its size, suggesting that the large area of these countries also contributes to their high numbers of naturalised species. (5) Countries with a long tradition in botanical research such as the United Kingdom, Belgium and the Czech Republic have made great efforts to monitor alien species (Celesti-Grapow et al. 2016; Kalusová et al. 2024), therefore, information availability is likely also uneven across countries. All these factors can be considered as reasons why certain countries harbour more alien species than others in our database (Arianoutsou et al. 2021).

A recent study using a large grass phylogenetic and geographical dataset suggests that C4 species are less likely than C3 species to colonise cold climates, such as continental, polar or alpine climates, because C4 species do not possess the ability to survive under prolonged cold conditions (Watcharamongkol et al. 2018). Therefore, it is somewhat surprising that we found a relatively high number of alien C4 species present in northern European countries (53 species). One possible explanation might be that the climate of these northern countries is more temperate than could be expected for such high latitudes due to the North Atlantic Current (Jóhannesson et al. 1995). The mild winters of maritime climates in Norway, Sweden, Denmark and Great Britain (Parsons and Lear 2001) provide a tolerable climate for C4 species (Hulme 2017; Clements and DiTommaso 2022). While northern Europe has the lowest total number of alien C4 grass species compared to other regions of Europe, it hosts the highest number of species in the casual category. This implies that besides climate other factors also influence the distribution of C4 grass species in this region. These countries are also amongst the countries with the most naturalised species (irrespective of the photosynthetic pathway) all over Europe (Pyšek et al. 2022a), indicating that many ecological and historical factors influence species establishment beyond climate.

4.2 | Alien Statuses per Region and Country

Europe is a highly dynamic landscape from the perspective of biological invasions. While a couple of decades ago southern European countries had more naturalised alien plant species than northern countries (Weber 1997), recent studies reported that most naturalised species were recorded in the northern part of the continent (Pyšek et al. 2022a). A similar dynamic can also be observed in the case of C4 grass species. Southern countries had outstanding numbers of naturalised species, indicating an advanced process of alien C4 grass species colonisation. In contrast, northern countries were characterised by the predominance of casual alien C4 grass species and a relatively low density, suggesting an early phase of colonisation. The western and eastern regions fell between with equal numbers of casual and naturalised species. This pattern is probably driven by two factors: residence time and climate change. The range size of alien species and the stage of invasion highly depend on how much time the species had to spread, i.e., its residence time, and on the intensity and frequency of introductions, i.e., propagule pressure (Wilson et al. 2007; Pyšek et al. 2009; Gioria et al. 2023). Western or southern Europe has a long history of plant introductions and a network of trade routes which facilitated the naturalisation and the subsequent invasion of these introduced C4 species several decades ago. Contrarily, northern Europe has plenty of casual species because of the short residence time and less suitable climates in the past.

Pyšek et al. (2022b) found that there is a weak positive correlation between the number of naturalised and invasive plant species in European mainland regions, and we also found a similar pattern in the case of southern and western Europe for alien C4 grass species. However, the number of casual species was not a good predictor of invasive species richness, perhaps due to the different traits that facilitate the establishment and the later spread of the species (Theoharides and Dukes 2007; Catford et al. 2019). We found that in southern and western Europe, the number of naturalised species is positively related to the number of invasive species. These patterns indicate that environmental or management factors in these regions might help species to progress from naturalisation to invasiveness. This is in line with previous studies (Chuine et al. 2012; Boretti and Florentine 2019), which indicate that warmer climates, higher propagule pressure, and more intensive land-use activities in these regions may facilitate the establishment and spread of alien species. The positive relationship between casual and invasive species observed in southern Europe might imply that the potential of casual species to progress towards invasiveness is facilitated by environmental factors and land use practices that favour their rapid establishment and spread. The weak relationship in eastern and northern Europe might be explained by climatic factors and different land use history and management practices in these regions, which could limit the progression of casual and naturalised species towards invasiveness.

The success of grasses in biological invasion can be related to the 'Viking syndrome', which postulates that invasive success is because of the efficient dispersal, rapid population growth, resilience to disturbance, phenotypic plasticity and the ability to transform environments to benefit the invader (Linder et al. 2018). According to these traits, C4 grass species are the most successful group concerning biological invasion worldwide (D'Antonio and Vitousek 1992). Their capacity to adapt to a wide range of conditions and transform environments could explain their dominance in regions such as southern and western Europe, where conditions are favourable for invasion (Chuine et al. 2012; Clements and DiTommaso 2022). The Viking syndrome may also explain the slower progression of alien species in northern Europe. In this region, harsher climates, shorter growing seasons and less historical propagule pressure may hinder traits that promote successful invasion.

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While the presence of naturalised and casual C4 grass species was common across Europe, only certain countries harboured a considerable number of invasive species. We found more than 10 invasive species in only four countries: Hungary, Romania, Spain and Italy. A common feature of these countries is on-going aridification and even desertification, driven by rainfall changes related to climate change and intense land-use changes in the last decades (especially in Hungary and Romania). These countries face changing soil water balance and sinking groundwater levels, leading to aridification particularly in summer, both in the Mediterranean region (Scocco et al. 2016), in Hungary (Kovács et al. 2017) and in the southern part of Romania (Prăvălie 2013). This aridification may have created favourable conditions for C4 grass species, potentially increasing their local abundance and distribution in these areas (Havrilla et al. 2023).

A great number of species (34 species) showed variations in statuses across different regions or even across countries within the same region. The context dependence of the invasion process might explain these differences (González-Moreno et al. 2014); however, the case of cryptic invasions cannot be neglected either. Cryptic invasions refer to those alien species that go unnoticed due to misidentification with a native or another alien species (Morais and Reichard 2018). Several C4 species have been reported to be easily confused with other similar species. For example, *Eleusine indica* with digitate inflorescences can be mistaken for other grasses with similar inflorescences (e.g., with *Digitaria* or *Cynodon*, Dítě et al. 2019). Similarly, Török et al. (2021) proved that *Sporobolus cryptandrus* has spread unnoticed and gained considerable distribution in Hungary. We consider the group of C4 grass species perfect candidates for cryptic invasions for three main reasons: (1) there are many introduced species from the same genera in Europe, which can easily go unnoticed in the early phases of invasion: 13 *Cenchrus* spp., 5 *Chloris* spp., 8 *Digitaria* spp., 7 *Echinochloa* spp., 21 *Eragrostis* spp., 8 *Panicum* spp., 8 *Setaria* spp., 16 *Sporobolus* spp.; (2) the distinction of the species of the Poaceae family is usually a greater challenge compared to species from other plant families; (3) C4 grass species mostly occur in man-made or ruderal habitats such as wastelands and modern agricultural landscapes, which are less frequently surveyed or even neglected by botanists (Edvardsen et al. 2010). Therefore, caution is needed in the interpretation of the present distribution of C4 grass species throughout Europe, as it is likely underestimated.

4.3 | The Most Widespread Alien C4 Grass Species in Europe

Several alien species have emerged and spread as weeds in agricultural habitats of Europe relatively rapidly within a few decades (Follak and Essl 2013). We can find the most widely distributed species in our database amongst these species: *Panicum* spp., *Setaria* spp., *Eleusine indica*, *Sorghum halepense*, etc. These species may have highly different invasion histories: archaeophytes repeatedly introduced for cultivation for over several hundreds or even thousands of years (Pyšek et al. 2022b) (*Panicum miliaceum*, *Setaria italica, Sorghum bicolor*) and accidentally or deliberately introduced neophytes present in the continent for less than 200 years (Pyšek et al. 2022b) (*Eleusine indica*, *Sorghum halepense, Panicum capillare*). However, the dynamic spread of both archaeophytes and neophytes is commonly influenced by their tolerance to herbicide application (Loddo et al. 2020; Vazquez-Garcia et al. 2020), changed agricultural practices, for example, intensified maize production, evolutionary changes of these weed species (Clements and Ditommaso 2011; Paterson et al. 2020) or their capability to take advantage of the ongoing climate change (Essl et al. 2009). The impact of these invasive species on crop yield can be significant in the invaded agricultural fields (*Sorghum halepense*, Follak and Essl 2013), and the aggravation of the phenomenon is assured by the human-assisted spread of these species via contaminated seeds.

4.4 | Origin and Habitat Preference of Alien C4 Grasses in Europe

Most alien species established in Europe are native to temperate Asia and America, mainly North America, due to similar climates and historical trade links between these continents (Pyšek et al. 2022b; Kalusová et al. 2024). Close climatic matching is a prerequisite of the alien species' establishment and naturalisation process (Richardson and Pyšek 2012). Interestingly, a considerable number of C4 grasses with tropical origins have become naturalised in different parts of Europe, which can often be explained by human activities mitigating climatic constraints. For example, many introduced ornamental plants of warmer regions need indoor overwintering for survival in the temperate zone. Such frequently cultivated ornamentals in Europe show now clear tendencies to escape cultivation (Rigó et al. 2023), for example, *Miscanthus sinensis* (Dougherty et al. 2014), *Stenotaphrum secundatum* (Englmaier and Wilhalm 2018), and *Eragrostis spectabilis* (Qing et al. 2013).

Many alien C4 species occur in disturbed and ruderal habitats, particularly in early phases of colonisation (Collins and Jones 1986; With 2002), and our results also confirm this. Other studies repeatedly emphasised the inability of C4 species to invade natural or semi-natural habitats even in later stages of colonisation in temperate regions (Minnesota, USA, Tilman 1997; southern part of New Zealand, White et al. 2001), showing instead high densities in ruderal habitats. Similarly, many European alien C4 grass species typically occur in highly disturbed habitats, for example, *Eragrostis minor*, *Eleusine indica*, *Cynodon dactylon*, *Setaria* spp., *Digitaria* spp. (Čarni and Mucina 1998). These results suggest an inferior competitive ability and superior disturbance tolerance of C4 species (White et al. 2001). However, recent field studies also emphasise that extreme climatic events, such as heat shocks, may reduce the competitive ability of the native resident C3 grass species, resulting in a die-back, which may enhance the colonisation ability of C4 grass species (Churchill et al. 2022). Consistent with this, an experimental study by Lemoine and Budny (2022) has also demonstrated that changes in soil moisture and seasonal productivity caused by warming enhanced the competitive advantage of C4 species in semi-natural or natural habitats. Therefore, colonisation of C4 grass species can be achieved at the expense of C3 grass species and other native species, which are declining in abundance due to changing climate (de Deus Vidal Jr. et al. 2021).

Another plausible explanation might be that there is a temporal niche separation between C3 and C4 grass species in temperate

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grasslands, and these two groups of species might coexist in grassland habitats: C3 species thrive in the cool spring and autumn, while C4 grass species are more active during the summer (Niu et al. 2008; Pau et al. 2013). However, with climate change, prolonged drought periods are expected to become more frequent even in spring and autumn (Witwicki et al. 2016), so C3 species may become increasingly vulnerable, and this may continue to give C4 grasses an edge. Such a scenario could potentially act to further increase the competitive pressures on C3 grasses, maybe even alter the species composition and dynamics. Therefore, rainfall seasonality should be tracked as an important factor that might determine a shift between C3 and C4 species in temperate regions (Havrilla et al. 2023).

4.5 | Temporal Changes in the C4 Grass Species List in Europe

Compared to the former lists of alien C4 grass species introduced to Europe (Collins and Jones 1986; Mateu 1992; Pyankov et al. 2010), we found considerably more introduced species: 71 totally new entries to the list and at least 25 species that are native to some parts of Europe but recently reported as alien in other countries. This considerable increase might be partly explained by the improved data sharing methods of species' distribution, ensuring data quality and integrity in online databases, and by the greatly improved national and international checklists of vascular plants which list species with corresponding synonyms and bibliographic details (Groom et al. 2017). Moreover, our intensive searching methods also contributed to this long species list, in contrast to former lists which were compiled based on a limited number of literature sources (Collins and Jones 1986; Mateu 1992; Pyankov et al. 2010). For example, *Sporobolus cryptandrus*, an invasive species with monodominant stands in Hungary (Török et al. 2021), was mentioned by none of the authors of the former lists, although it has had naturalised populations in Slovakia since 1987 and was repeatedly reported from other European countries as well (Holub and Jehlík 1987; Ryves 1988). As the C4 photosynthetic pathway was discovered only 50 years ago, the list of C4 species is continuously increasing due to phylogenetic clarifications and taxonomic revisions (Osborne et al. 2014), which could also contribute to the growing number of European C4 grass species. However, this significant increase in species numbers is probably also linked with direct or the indirect effects of climate change.

The European native range-expanding species category should be carefully treated, as it may include species that are introduced beyond their historic native range as a result of human actions or human-induced environmental changes, but may also include species that expand their ranges as a result of climate change (Essl et al. 2019). Species of the first category are legitimately termed as aliens and should be targeted by conservation actions, while species of the second category are refugees, and their survival must be aided.

5 | Conclusions and Outlook

Our study provided a comprehensive overview of the distribution, status, and habitat preferences of alien C4 grass species in Europe. Over the past 14 years, we observed a notable increase in the presence of these species compared to the list of Pyankov et al. (2010) (See also Appendix S1). We identified 133 species of alien C4 grasses in Europe, with the highest numbers found in western and southern Europe. The highest number of naturalised and invasive species in southern Europe may be associated with the strong anthropogenic influence in this region. Climate change-induced extreme events facilitate the establishment and invasion of C4 species, potentially creating vegetation gaps in ecosystems where native C3 grasses dominate, which may decline due to heat or drought stress. Trampled soils, roadsides, and agricultural areas are amongst the most invaded habitats, with some species also establishing in semi-natural and natural grassland habitats. Our findings underscore the vulnerability of grasslands to shifts in species composition due to complex interactions between human activities, climate change and invasion.

Based on our study, we suggest that long-term monitoring of plant invasion effects on ecological processes across different European regions is necessary to mitigate the future impact of C4 grass invasions. Further research into the temporal niche separation between C3 and C4 species, the specific mechanisms through which climate change facilitates invasions, and the socio-economic implication of these invasions is crucial. Our results highlight that coordinated efforts in research, monitoring, and management are needed to safeguard Europe's grassland ecosystems against the dual threats of climate change and biological invasions.

Author Contributions

Patricia Elizabeth Díaz Cando: conceptualisation (supporting); data curation (equal); investigation (equal), methodology (supporting), project administration (supporting); validation (supporting); visualisation (supporting); writing – original draft preparation; writing – review and editing (supporting). **Annamária Fenesi:** conceptualisation (supporting), data curation (supporting); investigation (supporting); validation (supporting); writing – review and editing (supporting). **Judit Sonkoly:** conceptualisation (supporting), data curation (supporting); funding acquisition (supporting); investigation (supporting); validation (supporting); visualisation (supporting); writing – review and editing (supporting). **Peliyagodage Chathura Dineth Perera:** conceptualisation (supporting); data curation (equal); investigation (equal), methodology (supporting), validation (supporting); writing – original draft preparation; writing – review and editing (supporting). **Péter Török:** conceptualisation (lead), data curation (equal); formal analysis; funding acquisition (lead); investigation (equal); methodology (lead); project administration (lead); validation (supporting); visualisation (lead); writing – original draft (lead); writing – review and editing (equal).

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Conflicts of Interest

The authors declare no conflicts of interest.

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Data Availability Statement

All the primary data used in the manuscript is provided in the Supporting Information and also stored on figshare (DOI: https://doi.org/10.6084/m9.figshare.28062287.v3).

References

Alcantara, R., P. Fernandez, R. J. Smeda, P. L. Alves, and R. De Prado. 2016. "Response of Eleusine Indica and *Paspalum distichum* to Glyphosate Following Repeated Use in Citrus Groves." *Crop Protection* 79: 1–7. https://doi.org/10.1016/j.cropro.2015.09.027.

Amare, T. 2016. "Review on Impact of Climate Change on Weed and Their Management." *American Journal of Biological and Environmental Statistics* 2: 21. https://doi.org/10.11648/j.ajbes.20160203.12.

Arianoutsou, M., I. Bazos, A. Christopoulou, et al. 2021. "Alien Plants of Europe: Introduction Pathways, Gateways and Time Trends." *PeerJ* 9: e11270. https://doi.org/10.7717/peerj.11270.

Bauer, N., and F. Verloove. 2023. "The Accelerated Spread of a Neophyte Introduced to Europe Long Ago–First Occurrence of *Sporobolus Indicus* (Poaceae) in Hungary." *Acta Botanica Croatica* 82: 20–26. https://doi.org/10.37427/botcro-2022-024.

Bernacki, Z. 2012. "Changes in the Balance Between C3 and C4 Plants Expected in Poland With the Global Change." *Ecological Questions* 16: 59–68. https://doi.org/10.2478/v10090-012-0006-2.

Blackburn, T. M., P. Pyšek, S. Bacher, et al. 2011. "A Proposed Unified Framework for Biological Invasions." *Trends in Ecology & Evolution* 26: 333–339. https://doi.org/10.1016/j.tree.2011.03.023.

Boretti, A., and S. Florentine. 2019. "Atmospheric CO_2 Concentration and Other Limiting Factors in the Growth of C 3 and C 4 Plants." *Plants* 8: 931–942. https://doi.org/10.3390/plants8040092.

Bouchenak-Khelladi, Y., G. A. Verboom, T. R. Hodkinson, et al. 2009. "The Origins and Diversification of C4 Grasses and Savanna-Adapted Ungulates." *Global Change Biology* 15, no. 10: 2397–2417. https://doi.org/10.1111/j.1365-2486.2009.01860.x.

Bradley, B. A., D. M. Blumenthal, D. S. Wilcove, and L. H. Ziska. 2010. "Predicting Plant Invasions in an Era of Global Change." *Trends in Ecology & Evolution* 25: 310–318. https://doi.org/10.1016/j.tree.2009.12.003.

Brunel, S., G. Schrader, G. Brundu, and G. Fried. 2010. "Emerging Invasive Alien Plants for the Mediterranean Basin." *EPPO Bulletin* 40: 219–238. https://doi.org/10.1111/j.1365-2338.2010.02378.x.

Burgiel, S. W., and A. A. Muir. 2010. *Invasive species, climate change and ecosystem-based adaptation: Addressing multiple drivers of global change.* Global Invasive Species Programme (GISP). https://doi.org/10.13140/2.1.1460.8161.

CABI. 2023. *Invasive Species - Detailed coverage of invasive species threatening livelihoods and the environment worldwide.* CABI Compendium. www.cabi.org/isc [Accessed 20 March 2023].

Cao Pinna, L., I. Axmanová, M. Chytrý, et al. 2021. "The Biogeography of Alien Plant Invasions in the Mediterranean Basin." *Journal of Vegetation Science* 32, no. 2: 1–13. https://doi.org/10.1111/jvs.12980.

Cao Pinna, L., L. Gallien, L. J. Pollock, et al. 2024. "Plant Invasion in Mediterranean Europe: Current Hotspots and Future Scenarios." *Ecography 2024* 2024: e07085. https://doi.org/10.1111/ecog.07085.

Capdevila-Argüelles, L., and B. Zilletti. 2008. *A perspective on climate change and invasive alien species*, 9–13. T-PVS/Inf. https://rm.coe.int/168074629c.

Čarni, A., and L. Mucina. 1998. "Vegetation of Trampled Soil Dominated by C4 Plants in Europe." *Journal of Vegetation Science* 9: 45–56. https://doi.org/10.2307/3237222.

Catford, J. A., and L. P. Jones. 2019. "Grassland Invasion in a Changing Climate. In Grasslands and Climate Change." In *Grasslands and Climate Change*, edited by D. J. Gibson and J. A. Newman, 149–171. Cambridge University Press. https://doi.org/10.1017/9781108163941.011.

Catford, J. A., A. Smith, P. Wragg, et al. 2019. "Traits Linked With Species Invasiveness and Community Invasibility Vary With Time, Stage and Indicator of Invasion in a Long-Term Grassland Experiment." *Ecology Letters* 22, no. 4: 593–604. https://doi.org/10.1111/ele.13220.

Catford, J. A., P. A. Vesk, D. M. Richardson, and P. Pyšek. 2012. "Quantifying Levels of Biological Invasion: Towards the Objective Classification of Invaded and Invasible Ecosystems." *Global Change Biology* 18: 44–62. https://doi.org/10.1111/j.1365-2486.2011.02549.x.

Celesti-Grapow, L., A. Alessandrini, P. V. Arrigoni, et al. 2009. "Inventory of the Non-native Flora of Italy." *Plant Biosystems* 143: 386–430. https://doi.org/10.1080/11263500902722824.

Celesti-Grapow, L., L. Bassi, G. Brundu, et al. 2016. "Plant Invasions on Small Mediterranean Islands: An Overview." *Plant Biosystems* 150: 1119–1133. https://doi.org/10.1080/11263504.2016.1218974.

Celesti-Grapow, L., and C. Ricotta. 2021. "Plant Invasion as an Emerging Challenge for the Conservation of Heritage Sites: The Spread of Ornamental Trees on Ancient Monuments in Rome, Italy." *Biological Invasions* 23: 1191–1206. https://doi.org/10.1007/s10530-020-02429-9.

Chuine, I., X. Morin, L. Sonié, et al. 2012. "Climate Change Might Increase the Invasion Potential of the Alien C4 Grass *Setaria Parviflora* (Poaceae) in the Mediterranean Basin." *Diversity and Distributions* 18: 661–672. https://doi.org/10.1111/j.1472-4642.2011.00880.x.

Churchill, A. C., H. Zhang, K. J. Fuller, et al. 2022. "Pastures and Climate Extremes: Impacts of Cool Season Warming and Drought on the Productivity of Key Pasture Species in a Field Experiment." *Frontiers in Plant Science* 13: 836968. https://doi.org/10.3389/fpls.2022.836968.

Chytrý, M., L. Tichý, S. M. Hennekens, et al. 2020. "EUNIS Habitat Classification: Expert System, Characteristic Species Combinations and Distribution Maps of European Habitats." *Applied Vegetation Science* 23: 648–675. https://doi.org/10.1111/avsc.12519.

Clements, D. R., and A. Ditommaso. 2011. "Climate Change and Weed Adaptation: Can Evolution of Invasive Plants Lead to Greater Range Expansion Than Forecasted?" *Weed Research* 51: 227–240. https://doi.org/10.1111/j.1365-3180.2011.00850.x.

Clements, D. R., and A. DiTommaso. 2022. "Climate change and the persistence of weeds." In: *Persistence Strategies of Weeds*, edited by M.K. Upadhyaya, D.R. Clements, and A. Shrestha, First Edition, 219–243. Hoboken, NJ: John Wiley & Sons. https://doi.org/10.1002/9781119525622.ch12.

Collins, R. P., and M. B. Jones. 1986. "The Influence of Climatic Factors on the Distribution of C4 Species in Europe." *Vegetatio* 64: 121–129. https://doi.org/10.1007/BF00044788.

Coppola, E., R. Nogherotto, J. M. Ciarlo, et al. 2021. "Assessment of the European Climate Projections as Simulated by the Large EURO-CORDEX Regional and Global Climate Model Ensemble." *Journal of Geophysical Research: Atmospheres* 126: e2019JD032356. https://doi.org/10.1029/2019jd032356.

D'Antonio, C. M., and P. M. Vitousek. 1992. "Biological invasions by exotic grasses, the grass/fire cycle, and global change." *Annual Review of Ecology and Systematics* 23: 63–87. https://www.jstor.org/stable/2097282.

de Deus Vidal, J., Jr., P. C. le Roux, S. D. Johnson, M. te Beest, and V. R. Clark. 2021. "Beyond the Tree-Line: The C3-C4 "Grass-Line" Can Track Global Change in the World's Grassy Mountain Systems." *Frontiers in Ecology and Evolution* 9: 760118. https://doi.org/10.3389/fevo.2021.760118.

Castro-Díez, P., A. Pauchard, A. Traveset, and M. Vilà. 2016. "Linking the Impacts of Plant Invasion on Community Functional Structure and Ecosystem Properties." *Journal of Vegetation Science* 27: 1233–1242. https://doi.org/10.1111/jvs.12429.

16541103, 2025, 2, Downloaded from https://onlinelibrary.wiley.com/doi/10.1111/jvs.70023 by University Of Debrecen, Wiley Online Library on [13/03/2025]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

Dítě, Z., D. Dítě, and V. Feráková. 2019. "*Eleusine indica* (L.) Gaertn., New Species of the Adventive Flora of Slovakia." *Thaiszia* 29: 77–84. https://doi.org/10.33542/TJB2019-1-06.

Dougherty, R., L. Quinn, A. Endres, T. Voigt, and J. Barney. 2014. "Natural History Survey of the Ornamental Grass *Miscanthus Sinensis* in the Introduced Range." *Invasive Plant Science and Management* 7: 113–120. https://doi.org/10.1614/IPSM-D-13-00037.1.

Drobinski, P., N. Da Silva, S. Bastin, et al. 2020. "How Warmer and Drier Will the Mediterranean Region Be at the End of the Twenty-First Century?" *Regional Environmental Change* 20: 78. https://doi.org/10.1007/s10113-020-01659-w.

Edvardsen, A., R. Halvorsen, A. Norderhaug, O. Pedersen, and K. Rydgren. 2010. "Habitat Specificity of Patches in Modern Agricultural Landscapes." *Landscape Ecology* 25: 1071–1083. https://doi.org/10.1007/s10980-010-9481-2.

Edwards, G. E., and E. V. Voznesenskaya. 2011. "Chapter 4 C4 photosynthesis: Kranz forms and single-cell C4 in terrestrial plants." In *C4 Photosynthesis and Related CO2 Concentrating Mechanisms*, edited by A. Raghavendra and R. Sage, 32, 29–61. Dordrecht, Netherlands: Springer. https://doi.org/10.1007/978-90-481-9407-0_4.

Englmaier, P., and T. Wilhalm. 2018. "Alien Grasses (Poaceae) in the Flora of the Eastern Alps: Contribution to an Excursion Flora of Austria and the Eastern Alps." *Neiřofiziologiia* 9: 177–245. https://www.zobodat.at/pdf/NEIL_9_0177-0245.pdf.

Essl, F., S. Dullinger, P. Genovesi, et al. 2019. "A Conceptual Framework for Range-Expanding Species That Track Human-Induced Environmental Change." *Bioscience* 69: 908–919. https://doi.org/10.1093/biosci/biz101.

Essl, F., M. Staudinger, O. Stöhr, L. Schratt-Ehrendorfer, W. Rabitsch, and H. Niklfeld. 2009. "Distribution Patterns, Range Size and Niche Breadth of Austrian Endemic Plants." *Biological Conservation* 142: 2547–2558. https://doi.org/10.1016/j.biocon.2009.05.027.

Euro+Med. 2023. "EDIT-European Distributed Institute of Taxonomy". https://europlusmed.org/node/129 [Accessed 10 February 2023]. Retrieved from:

European Environment, A. 2017. "Climate Change, Impacts and Vulnerability in Europe 2016–An Indicator-Based Report." EEA Report No. 1/2017. Luxermbourg: Publications Office of the European Union. https://www.eea.europa.eu/publications/climate-change-impacts-and-vulnerability-2016.

European Environment Agency. 2021. *What will the future bring when it comes to climate hazards?–Overview*, 1–7. Retrieved from. European Environment Agency. https://www.eea.europa.eu/publications/europes-changing-climate-hazards-1/what-will-the-future-bring.

Fernando, N., S. Manalil, S. Florentine, B. Chauhan, and S. Seneweera. 2016. "Glyphosate Resistance of C3 and C4 Weeds Under Rising Atmospheric CO_2." *Frontiers in Plant Science* 7: 910. https://doi.org/10.3389/fpls.2016.00910.

Finch, D. M., J. L. Butler, J. B. Runyon, et al. 2021. "Effects of Climate Change on Invasive Species." In *Invasive Species in Forests and Rangelands of the United States*, edited by T. M. Poland, T. Patel-Weynand, D. M. Finch, C. F. Miniat, D. C. Hayes, and V. M. Lopez, 57–83. Champ: Springer. https://doi.org/10.1007/978-3-030-45367-1_4.

Follak, S., and F. Essl. 2013. "Spread Dynamics and Agricultural Impact of *Sorghum Halepense*, an Emerging Invasive Species in Central Europe." *Weed Research* 53: 53–60. https://doi.org/10.1111/j.1365-3180.2012.00952.x.

GBIF. 2023. "GBIF|Global Biodiversity Information Facility". https://www.gbif.org/species/6 [Accessed 30 October 2023]. Retrieved from.

Gentili, R., R. Ambrosini, B. Augustinus, et al. 2021. "High Phenotypic Plasticity in a Prominent Plant Invader Along Altitudinal and Temperature Gradients." *Plants* 10: 2144. https://doi.org/10.3390/plants10102144.

Gioria, M., P. E. Hulme, D. M. Richardson, and P. Pyšek. 2023. "Why Are Invasive Plants Successful?" *Annual Review of Plant Biology* 74: 635–670. https://doi.org/10.1146/annurev-Arplant-070522-071021.

GLONAF. 2023. "The Global Naturalized Alien Flora (GloNAF) database". https://sebastian-ch.github.io/glonafAtlas/plantView/index.html [Accessed 28 January 2023]. Retrieved from.

González-Moreno, P., J. M. Diez, I. Ibáñez, X. Font, and M. Vilà. 2014. "Plant Invasions Are Context-Dependent: Multiscale Effects of Climate, Human Activity and Habitat." *Diversity and Distributions* 20: 720–731. https://doi.org/10.1111/ddi.12206.

Griffith, D. M., T. M. Anderson, C. P. Osborne, C. A. Strömberg, E. J. Forrestel, and C. J. Still. 2015. "Biogeographically Distinct Controls on C3 and C4 Grass Distributions: Merging Community and Physiological Ecology." *Global Ecology and Biogeography* 24: 304–313. https://doi.org/10.1111/geb.12265.

Gritti, E. S., B. Smith, and M. T. Sykes. 2006. "Vulnerability of Mediterranean Basin Ecosystems to Climate Change and Invasion by Exotic Plant Species." *Journal of Biogeography* 33: 145–157. https://doi.org/10.1111/j.1365-2699.2005.01377.x.

Groom, Q., L. Weatherdon, and I. Geijzend. 2017. "Is Citizen Science an Open Science in the Case of Biodiversity Observations?" *Journal of Applied Ecology* 54: 612–617. https://doi.org/10.1111/1365-2664.12767.

Havrilla, C. A., J. B. Bradford, C. B. Yackulic, and S. M. Munson. 2023. "Divergent Climate Impacts on C3 Versus C4 Grasses Imply Widespread 21st Century Shifts in Grassland Functional Composition." *Diversity and Distributions* 29: 379–394. https://doi.org/10.1111/ddi.13669.

Holub, J., and V. Jehlík. 1987. "*Sporobolus Cryptandrus* in Czechoslovakia [in Czech]." *Preslia* 59: 117–134. https://www.preslia.cz/article/11292.

Hulme, P. E. 2017. "Climate Change and Biological Invasions: Evidence, Expectations, and Response Options." *Biological Reviews* 92: 1297–1313. https://doi.org/10.1111/brv.12282.

IPCC. 2023. "Climate Change 2023: Synthesis Report." In *Contribution of Working Groups I, II and III to the Sixth Assessment Report of the Intergovernmental Panel on Climate Change.* Core Writing Team, edited by H. Lee and J. Romero, 184. IPCC. https://doi.org/10.59327/IPCC/AR6-9789291691647.

Jia, J., Z. Dai, F. Li, and Y. Liu. 2016. "How Will Global Environmental Changes Affect the Growth of Alien Plants?" *Frontiers in Plant Science* 7: 1623. https://doi.org/10.3389/fpls.2016.01623.

Jóhannesson, T., T. Jónsson, E. Källén, and E. Kaas. 1995. "Climate change scenarios for the Nordic countries." *Climate Research* 5: 181–195. https://doi.org/10.3354/cr005181.

Kalusová, V., N. Čeplová, J. Danihelka, et al. 2024. "Alien plants of Europe: an overview of national and regional inventories." *Preslia* 96: 149–182. https://doi.org/10.23855/preslia.2024.149.

Kovács, A. D., E. Hoyk, and J. Z. Farkas. 2017. "Homokhátság-a Special Rural Area Affected by Aridification in the Carpathian Basin, Hungary." *European Countryside* 9: 29–50. https://doi.org/10.1515/euco-2017-0003.

Kovats, R. S., R. Valentini, L. M. Bouwer, et al. 2014. *Climate Change 2014: Impacts, Adaptation and Vulnerability: Part B: Regional Aspects: Working Group II Contribution to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change*, edited by Barros, V. R., Field, C. B., Dokken, D. J., et al., 1267–1326. Cambridge, UK and NY: Cambridge University Press. https://doi.org/10.1017/CBO9781107415386.003.

Kumar, V., A. Sharma, J. K. Soni, and N. Pawar. 2017. "Physiological Response of C3, C4 and CAM Plants in Changeable Climate." *Pharmaceutical Innovation* 6: 70. https://www.proquest.com/scholarly-journals/physiological-response-c3-c4-cam-plants/docview/1937785326/se-2.

Law, R. D., and S. J. Crafts-Brandner. 2001. "High Temperature Stress Increases the Expression of Wheat Leaf Ribulose-1, 5-Bisphosphate

16541103, 2025, 2, Downloaded from https://onlinelibrary.wiley.com/doi/10.1111/jvs.70023 by University Of Debrecen, Wiley Online Library on [13/03/2025]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

Carboxylase/Oxygenase Activase Protein." *Archives of Biochemistry and Biophysics* 386: 261–267. https://doi.org/10.1006/abbi.2000.2225.

Lee, H., K. Calvin, D. Dasgupta, et al. 2023. "IPCC, 2023: Climate Change 2023: Synthesis Report, Summary for Policymakers." In *Contribution of Working Groups I, II and III to the Sixth Assessment Report of the Intergovernmental Panel on Climate Change*. Core Writing Team, edited by H. Lee and J. Romero. IPCC. https://doi.org/10.59327/IPCC/AR6-9789291691647.00.

Lemoine, N. P., and M. L. Budny. 2022. "Seasonal Soil Moisture Variability, Not Drought, Drives Differences in Photosynthetic Physiology of Two C4 Grass Species." *Plant Ecology* 223: 627–642. https://doi.org/10.1007/s11258-022-01236-7.

Lewandowski, I., J. M. Scurlock, E. Lindvall, and M. Christou. 2003. "The Development and Current Status of Perennial Rhizomatous Grasses as Energy Crops in the US and Europe." *Biomass and Bioenergy* 25: 335–361. https://doi.org/10.1016/S0961-9534(03)00030-8.

Linder, H. P., C. E. Lehmann, S. Archibald, C. P. Osborne, and D. M. Richardson. 2018. "Global Grass (Poaceae) Success Underpinned by Traits Facilitating Colonization, Persistence and Habitat Transformation." *Biological Reviews* 93: 1125–1144. https://doi.org/10.1111/brv.12388.

Loddo, D., G. Imperatore, A. Milani, et al. 2020. "First Report of Glyphosate-Resistant Biotype of *Eleusine Indica* (L.) Gaertn. In Europe." *Agronomy* 10, no. 11: 1692. https://doi.org/10.3390/agronomy10111692.

Lopes, A., L. Demarchi, M. Piedade, et al. 2023. "Predicting the Range Expansion of Invasive Alien Grasses Under Climate Change in the Neotropics." *Perspectives in Ecology and Conservation* 21: 128–135. https://doi.org/10.1016/j.pecon.2023.02.005.

Mateu, A. 1992. "A Revised List of the European C4 Plants." *Photosynthetica* 26: 323–331.

Morais, P., and M. Reichard. 2018. "Cryptic Invasions: A Review." *Science of the Total Environment* 613: 1438–1448. https://doi.org/10.1016/j.scitotenv.2017.06.133.

Navarra, A., and L. Tubiana, eds. 2013. *Regional Assessment of Climate Change in the Mediterranean*. Vol. 3: Case Studies, 225. Springer Science.

Niu, S., W. Liu, and S. Wan. 2008. "Different Growth Responses of C3 and C4 Grasses to Seasonal Water and Nitrogen Regimes and Competition in a Pot Experiment." *Journal of Experimental Botany* 59: 1431–1439. https://doi.org/10.1093/jxb/ern051.

Olden, J. D., N. L. Poff, M. R. Douglas, M. E. Douglas, and K. D. Fausch. 2004. "Ecological and Evolutionary Consequences of Biotic Homogenization." *Trends in Ecology & Evolution* 19: 18–24. https://doi.org/10.1016/j.tree.2003.09.010.

Osborne, C. P., A. Salomaa, T. A. Kluyver, et al. 2014. "A Global Database of C4 Photosynthesis in Grasses." *New Phytologist* 204: 441–446. https://doi.org/10.1111/nph.12942.

Parsons, L. S., and W. H. Lear. 2001. "Climate Variability and Marine Ecosystem Impacts: A North Atlantic Perspective." *Progress in Oceanography* 49: 167–188. https://doi.org/10.1016/S0079-6611(01)00021-0.

Paterson, A. H., W. Kong, R. M. Johnston, et al. 2020. "The Evolution of an Invasive Plant, *Sorghum halepense* L.('Johnsongrass')." *Frontiers in Genetics* 11: 317. https://doi.org/10.3389/fgene.2020.00317.

Pau, S., E. J. Edwards, and C. J. Still. 2013. "Improving Our Understanding of Environmental Controls on the Distribution of C3 and C4 Grasses." *Global Change Biology* 19: 184–196. https://doi.org/10.1111/gcb.12037.

POWO. 2023. *Plants of the World Online. Facilitated by the Royal Botanic Gardens, Kew.* Published on the Internet. http://www.plantsoftheworldonline.org/ [Accessed July 15 2023].

Prăvălie, R. 2013. "Climate Issues on Aridity Trends of Southern Oltenia in the Last Five Decades." *Geographia Technica* 1: 70–79. https://www.technicalgeography.org/pdf/1_2013/08_1_2013.pdf.

Pyankov, V. I., H. Ziegler, H. Akhani, C. Deigele, and U. Lüttge. 2010. "European Plants With C 4 Photosynthesis: Geographical and Taxonomic Distribution and Relations to Climate Parameters." *Botanical Journal of the Linnean Society* 163: 283–304. https://academic.oup.com/botlinnean/article/163/3/283/2418469.

Pyšek, P., M. Křivánek, and V. Jarošík. 2009. "Planting Intensity, Residence Time, and Species Traits Determine Invasion Success of Alien Woody Species." *Ecology* 90: 2734–2744. https://doi.org/10.1890/08-0857.1.

Pyšek, P., J. Pergl, W. Dawson, et al. 2022a. "European Plant Invasions." In *Global Plant Invasions*, edited by D. R. Clements, M. K. Upadhyaya, S. Joshi, and A. Shrestha, 151–165. Springer International Publishing. https://doi.org/10.1007/978-3-030-89684-3_7.

Pyšek, P., J. Sádlo, J. Chrtek Jr, et al. 2022b. "Catalogue of Alien Plants of The Czech Republic (3rd Edition)." *Preslia* 94, no. 4: 447–577. https://doi.org/10.23855/preslia.2022.447.

Qing, Y., J. Wu, and X. Yuan. 2013. "Seed Germination Characteristics of Ornamental Grass *Eragrostis Spectabilis* (Poaceae)." *Plant Diversity and Resources* 35: 165–170. https://doi.org/10.7677/ynzwyj201312072.

R Core Team. 2023. *R: A Language and Environment for Statistical Computing. Version 4.3.2*. R Foundation for Statistical Computing.

Richardson, D. M., and P. Pyšek. 2012. "Naturalization of Introduced Plants: Ecological Drivers of Biogeographical Patterns." *New Phytologist* 196: 383–396. https://doi.org/10.1111/j.1469-8137.2012.04292.x.

Richardson, D. M., P. Pyšek, M. Rejmánek, M. G. Barbour, F. Dane Panetta, and C. J. West. 2000. "Naturalization and Invasion of Alien Plants: Concepts and Definitions." *Diversity and Distributions* 6: 93–107. https://doi.org/10.1046/j.1472-4642.2000.00083.x.

Rigó, A., Á. Malatinszky, and Z. Barina. 2023. "Inventory of the Urban Flora of Budapest (Hungary) Highlighting New and Noteworthy Floristic Records." *Biodiversity Data Journal* 11: e110450. https://doi.org/10.3897/BDJ.11.e110450.

Robinson, T. B., N. Martin, T. G. Loureiro, P. Matikinca, and M. P. Robertson. 2020. "Double Trouble: The Implications of Climate Change for Biological Invasions." *NeoBiota* 62: 463–487. https://neobiota.pensoft.net/article/55729/.

Ryves, T. B. 1988. "Supplementary List of Wool-Alien Grasses Recorded From Blackmoor, North Hants., 1959–1976." *Watsonia* 17: 76–79. https://archive.bsbi.org.uk/Wats17p73.pdf.

Sage, R. F., and D. S. Kubien. 2003. "Quo Vadis C4? An Ecophysiological Perspective on Global Change and the Future of C4 Plants." *Photosynthesis Research* 77: 209–225. https://doi.org/10.1023/A:1025882003661.

Sales, C. R., Y. Wang, J. B. Evers, and J. Kromdijk. 2021. "Improving C4 Photosynthesis to Increase Productivity Under Optimal and Suboptimal Conditions." *Journal of Experimental Botany* 72: 5942–5960. https://doi.org/10.1093/jxb/erab327.

Salesse-Smith, C., N. Adar, B. Kannan, et al. 2025. "Adapting C4 Photosynthesis to Atmospheric Change and Increasing Productivity by Elevating Rubisco Content in Sorghum and Sugarcane." *Proceedings of the National Academy of Sciences* 122: e2419943122. https://doi.org/10.1073/pnas.2419943122.

Scocco, P., K. Piermarteri, A. Malfatti, F. M. Tardella, and A. Catorci. 2016. "Increase of Drought Stress Negatively Affects the Sustainability of Extensive Sheep Farming in Sub-Mediterranean Climate." *Journal of Arid Environments* 128: 50–58. https://doi.org/10.1016/j.jaridenv.2016.01.006.

Singh, R., A. K. Singh, P. Rajak, and H. Singh. 2023. "Plant invasion and climate change: An overview on history, impacts, and management practices." In *Plant Invasions and Global Climate Change*, edited by S. Tripathi, R. Bhadouria, P. Srivastava, R. Singh, and D. R. Batish, 343–365. Springer. https://doi.org/10.1007/978-981-99-5910-5_15.

16541103, 2025, 2, Downloaded from https://onlinelibrary.wiley.com/doi/10.1111/jvs.70023 by University Of Debrecen, Wiley Online Library on [13/03/2025]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

Šmilauer, P., and J. Lepš. 2014. *Multivariate Analysis of Ecological Data Using CANOCO 5*. 2nd ed. Cambridge University Press.

Sonkoly, J., E. Tóth, N. Balogh, et al. 2023. "PADAPT 1.0–the Pannonian Dataset of Plant Traits." *Scientific Data* 10: 742. https://doi.org/10.1038/s41597-023-02619-9.

Theoharides, K., and J. Dukes. 2007. "Plant Invasion Across Space and Time: Factors Affecting Nonindigenous Species Success During Four Stages of Invasion." *New Phytologist* 176: 256–273. https://doi.org/10.1111/j.1469-8137.2007.02207.x.

Thuiller, W., D. M. Richardson, and G. F. Midgley. 2008. "Will Climate Change Promote Alien Plant Invasions?" In *Biological Invasions*. Ecological Studies, edited by W. Nentwig, vol. 193, 197–211. Springer. https://doi.org/10.1007/978-3-540-36920-2_12.

Tilman, D. 1997. "Community Invasibility, Recruitment Limitation, and Grassland Biodiversity." *Ecology* 78: 81–92. https://doi.org/10.1890/0012-9658(1997)078[0081:CIRLAG]2.0.CO;2.

Török, P., and E. Aradi. 2017. "A New Potentially Invasive Grass, Sand Dropseed (*Sporobolus Cryptandrus*) Discovered in Sandy Areas of Hungary–A Call for Information on New Localities." *Bulletin of the Eurasian Dry Grassland Group* 35: 24–25.

Török, P., D. Schmidt, Z. Bátori, et al. 2021. "Invasion of the North American Sand Dropseed (*Sporobolus cryptandrus*)–A New Pest in Eurasian Sand Areas?" *Global Ecology and Conservation* 32: e01942. https://doi.org/10.1016/j.gecco.2021.e01942.

United Nations Geoscheme. 2024. https://unstats.un.org/unsd/methodology/m49/. [Accessed 14 July 2024].

Uprety, D. C., N. Dwivedi, V. Jain, and R. Mohan. 2002. "Effect of Elevated Carbon Dioxide Concentration on the Stomatal Parameters of Rice Cultivars." *Photosynthetica* 40: 315–319. https://doi.org/10.1023/A:1021322513770.

Vazquez-Garcia, J. G., C. Palma-Bautista, A. M. Rojano-Delgado, R. De Prado, and J. Menendez. 2020. "The First Case of Glyphosate Resistance in Johnsongrass (*Sorghum Halepense* (L.) Pers.) in Europe." *Plants* 9: 313. https://doi.org/10.3390/plants9030313.

Vilà, M., J. D. Corbin, J. S. Dukes, J. Pino, and S. D. Smith. 2007. "Linking Plant Invasions to Global Environmental Change." In *Terrestrial Ecosystems in a Changing World*, edited by J. G. Canadell, D. E. Pataki, and L. F. Pitelka, 93–102. Global Change–The IGBP Series. Springer. https://doi.org/10.1007/978-3-540-32730-1_8.

Walther, G. R., A. Roques, P. E. Hulme, et al. 2009. "Alien Species in a Warmer World: Risks and Opportunities." *Trends in Ecology & Evolution* 24: 687–693. https://doi.org/10.1016/j.tree.2009.06.008.

Wang, F., J. Gao, J. W. Yong, Q. Wang, J. Ma, and X. He. 2020. "Higher Atmospheric CO_2 Levels Favor C3 Plants Over C4 Plants in Utilizing Ammonium as a Nitrogen Source." *Frontiers in Plant Science* 11: 537443. https://doi.org/10.3389/fpls.2020.537443.

Watcharamongkol, T., P. A. Christin, and C. P. Osborne. 2018. "C4 Photosynthesis Evolved in Warm Climates but Promoted Migration to Cooler Ones." *Ecology Letters* 21: 376–383. https://doi.org/10.1111/ele.12905.

Weber, E. F. 1997. "The Alien Flora of Europe: A Taxonomic and Biogeographic Review." *Journal of Vegetation Science* 8: 565–572. https://doi.org/10.2307/3237208.

White, T. A., B. D. Campbell, P. D. Kemp, and C. L. Hunt. 2001. "Impacts of Extreme Climatic Events on Competition During Grassland Invasions." *Global Change Biology* 7: 1–13. https://doi.org/10.1046/j.1365-2486.2001.00381.x.

Wilson, J. R., D. M. Richardson, M. Rouget, et al. 2007. "Residence Time and Potential Range: Crucial Considerations in Modelling Plant Invasions." *Diversity and Distributions* 13: 11–22. https://doi.org/10.1111/j.1366-9516.2006.00302.x.

With, K. A. 2002. "The Landscape Ecology of Invasive Spread." *Conservation Biology* 16: 1192–1203. https://doi.org/10.1046/j.1523-1739.2002.01064.x.

Witwicki, D. L., S. M. Munson, and D. P. Thoma. 2016. "Effects of Climate and Water Balance Across Grasslands of Varying C3 and C4 Grass Cover." *Ecosphere* 7: e01577. https://doi.org/10.1002/ecs2.1577.

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